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Diets and growth potential of early stage larval yellow perch and alewife in a nearshore region of southeastern Lake Michigan

Jonah L. Withers [a,*,1], Timothy M. Sesterhenn [a,2], Carolyn J. Foley [a,b], Cary D. Troy [c], Tomas O. Höök [a,b]

[a] Department of Forestry and Natural Resources, College of Agriculture, Purdue University, 195 Marsteller Street, West Lafayette, IN 47907, USA
[b] Illinois-Indiana Sea Grant, 195 Marsteller Street, West Lafayette, IN 47907, USA
[c] School of Civil Engineering, Purdue University, 550 Stadium Mall Drive, West Lafayette, IN 47907, USA

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ABSTRACT

Transition from endogenous to exogenous feeding is thought to be a critical period for many fish larvae, when prey availability (type, size, and density) and ambient physical conditions (e.g., temperature, water clarity) can strongly influence survival. In Lake Michigan, two important fish species, yellow perch (*Perca flavescens*) and alewife (*Alosa pseudoharengus*), hatch and, presumably, begin exogenously feeding in the nearshore zone, an area characterized by short-term variation in environmental conditions. During 2010-2011, we examined environmental conditions and spatial and temporal distributions of larval yellow perch, larval alewife, and their potential prey in a nearshore region of southeastern Lake Michigan. To consider implications of environmental conditions on larval fish habitat quality, we quantified diet contents of young larval yellow perch and alewife and modeled bioenergetic growth rate potential (an index of habitat quality) under observed and predicted prey consumption scenarios. As expected, in this dynamic nearshore zone temperatures, light levels, zooplankton prey availability, and resulting growth rate potential were highly variable. Many larval fish digestive tracts were empty, suggesting that starvation may affect cohort survival. Among early-feeding larval fish, relatively small diet items were common, with larval alewives consuming diatoms and larval yellow perch consuming veligers of invasive dreissenid mussels. Though the mechanisms underlying such prey consumption and the consequences of ingesting these prey items remain largely unexplored, our results suggest dreissenid mussel veligers present early-feeding larvae with a relatively abundant prey source that may partially offset the apparent low consumption of other prey sources within Lake Michigan's nearshore region.

Introduction

Annual recruitment success of many fish populations is set during early-life when abundance is high and survival is relatively low. The interaction of abiotic and biotic mechanisms structuring early-life survival and eventual recruitment to the adult population are often not fully understood and highly variable among systems and over time (Claramunt and Wahl, 2000; Hjort, 1914; Houde, 1996). While ultimate survival through early life involves surviving a series of ontogenetic stanzas with potentially differing controlling factors (Pepin and Myers, 1991), predation and starvation are two key processes that frequently affect survival of young fishes. Both these processes are strongly regulated by individual growth rates and size. As fish grow, they become less susceptible to starvation due to relatively high energy stores, have lower mass-specific metabolic rates, and have enhanced abilities to capture a diversity of prey. Similarly, risk of predation generally decreases as fish grow, as greater size and faster swimming speeds allow fish to escape gape-limited predators (e.g., Miller et al., 1988; Pepin, 1989). Feeding success and resulting growth rates, which regulate starvation and predation risk, are in turn affected by a suite of environmental factors including temperature, water clarity, and availability of prey (Houde, 1996; Letcher et al., 1996). In particular, for many fish larvae the transition from endogenous to exogenous feeding may represent a critical period for survival (Miller et al., 1988; Sifa and Mathias, 1987).

In Lake Michigan, USA, yellow perch (*Perca flavescens*) and alewife (*Alosa pseudoharengus*) are abundant components of the fish community and contribute either directly (yellow perch) or indirectly (alewife, as forage for piscivores) to economically important fisheries. Both species have experienced variable recruitment success in Lake Michigan over the past few decades (Clapp and Dettmers, 2004; Francis et al., 1996; Madenjian et al., 2005; Wells, 1977). Recruitment of yellow perch in Lake Michigan appears to be set during the first 60 days of life (Robillard et al., 1999), and recruitment success has been related to many factors, including fishing-induced changes in spawning stock

* Corresponding author.
E-mail address: jonahlawrencewithers@gmail.com (J.L. Withers).
[1] Present address: US Fish and Wildlife Service, 308 Washington Avenue, Lamar, Pennsylvania, 16848, USA.
[2] Present address: Department of Biology and Chemistry, Morningside College, 1501 Morningside Avenue, Sioux City, Iowa, 51106, USA.

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composition (Headley and Lauer, 2008; Heyer et al., 2001; Wilberg et al., 2005), change in zooplankton assemblages (Dettmers et al., 2003; Redman et al., 2011; Weber et al., 2011), predation by alewives (Redman et al., 2011; Shroyer and McComish, 2000; Weber et al., 2011), and variable temperature regimes (Redman et al., 2011; Weber et al., 2011). Recruitment success of alewife across the Great Lakes is also highly variable and seemingly influenced by diverse factors (Jude and Tesar, 1985; Madenjian et al., 2005; O'Gorman et al., 2004). Madenjian et al. (2005) evaluated potential drivers of alewife recruitment in Lake Michigan from 1962 to 2002 and found that adult stock size, predation by salmonines, and spring–summer temperatures during the first year of life collectively affected alewife recruitment to age-3. Larval alewife appear to grow faster and survive better in a warm environment with dense small zooplankton (i.e., Muskegon Lake, a drowned river mouth lake), as compared to a cool environment with less small-bodied prey (i.e., nearshore Lake Michigan; Höök et al., 2007).

The majority of larval yellow perch and alewife in Lake Michigan hatch and presumably begin exogenous feeding in the nearshore zone (<20 m) (Höök et al., 2008; Jude et al., 1981; Perrone et al., 1983; Wells, 1973) where environmental conditions (e.g., temperature, water clarity, zooplankton densities) are relatively unstable and characterized by high spatial and temporal heterogeneity (Ayers et al., 1958; Mortimer, 2004; Troy et al., 2012). Past studies indicate that larval yellow perch and alewife growth and survival are responsive to ambient prey (Graeb et al., 2004; Heinrich, 1981), light, (Blaxter, 1986; Wellington et al., 2010) and temperature conditions (Edsall, 1970; Fry, 1971). First-feeding yellow perch expressed higher growth and survival when fed copepod nauplii, and did not survive when only provided adult copepods or cladocerans (Graeb et al., 2004). Not surprisingly, unfed larval alewife grow slower than fed larval alewife and may die between 2 and 7 days post-hatch, depending on ambient temperature (Edsall, 1970; Heinrich, 1981). Furthermore, water clarity has been shown to influence prey capture efficiency of larval yellow perch (Martin et al., 2012), and temperature is well established to affect various aspects of larval fish feeding and growth (Edsall, 1970; Fry, 1971).

Early stage larval yellow perch and alewife are relatively poor swimmers and their movement is essentially passive and strongly influenced by water currents (Höök et al., 2006; Houde, 1969; Klumb et al., 2003). Past studies have highlighted the potential importance of offshore advection of larval yellow perch in Lake Michigan, suggesting that in the past, lower predation pressure and availability of large-bodied zooplankton prey may have provided an advantage to individuals advected to offshore waters (e.g. Dettmers et al., 2003, 2005; Shroyer and McComish, 2000; Weber et al., 2011). However, depending on the timing of larval emergence, rapid changes in the nearshore environment may either expose larvae to warm temperatures, suitable water clarities and high densities of appropriate prey, facilitating a successful transition to exogenous feeding, high survival and adequate growth, or lead larval fish to experience less favorable conditions, leading to limited prey consumption, poor survival and slow growth.

Contemporary assessments of nearshore environmental conditions, prey consumption, and growth potential of larval yellow perch and alewife are important as the Lake Michigan ecosystem has fundamentally changed over the past 30 years. Earlier assessments of larval fish dynamics in the nearshore zone (e.g., Jude et al., 1981) may not be reflective of current dynamics, where reduced nutrient loading (Han and Allan, 2012; Lehman et al., 2013) and the proliferation of invasive species, most notably *Dreissena polymorpha* and *D. rostriformis bugensis* (hereafter dreissenids), have contributed to increased water clarity (Bunnell et al., 2014) and altered phytoplankton (Mida et al., 2010) and zooplankton (Pothoven and Fahnenstiel, 2015; Vanderploeg et al., 2012) assemblages. Moreover, differences in larval fish performance between nearshore and offshore hypothesized in the past (Dettmers et al., 2005) may not hold under this altered ecosystem. We assessed the effects of environmental conditions in a nearshore region of southeastern Lake Michigan on larval yellow perch and alewife by 1) characterizing water clarity, temperature, and zooplankton abundance, 2) evaluating diets of larval fishes as they transition from endogenous to exogenous feeding, and 3) evaluating the potential effects of temperature, light, and prey type on habitat quality using a bioenergetics approach. We expected that our results would provide insight as to mechanisms affecting growth and survival in this potentially important nursery area for first-feeding larval fish.

Methods

Field collections and laboratory processing

We sampled larval fish, zooplankton, temperature, and water clarity along a transect perpendicular to shore in Lake Michigan near Michigan City, IN, USA (Fig. 1). During daylight, we collected larval fish, zooplankton, and Secchi depth every 3–4 days from April to August of 2010 and once per week from April to August of 2011, and we deployed instruments to continuously monitor temperature and water clarity. We assessed variability in temperature by deploying three thermistor strings at depths of 15 m, 18 m, and 21 m. The 15 and 18 m string locations coincided with the center points of our ichthyoplankton sampling areas (see below; Fig. 1). Thermistor strings were deployed from day-of-year (DOY) 125–286 in 2010 and DOY 126–269 in 2011. Each thermistor string consisted of an anchored chain attached to a surface buoy, with temperature loggers attached every two meters from surface to bottom. Temperature loggers recorded temperature (°C) every 10 min while deployed. We measured water clarity continuously with a light meter that was attached at the bottom near the anchor of the thermistor string set at the 15 m depth contour. We used these measures to calculate mean daily transparency over 24 h intervals. We also used a Secchi disk to measure water clarity on each sampling day at three center points of our ichthyoplankton towing tracks (7 m, 15 m, and 18 m; see below and Fig. 1).

At the center point of the 15 m towing track (see below), potential zooplankton prey were collected via two replicate, vertical tows of a 0.5 m diameter, 2.0 m long, 64 μm mesh zooplankton net from ~0.5 m above the bottom to the surface at 0.2 m s^{-1}. Zooplankton samples were concentrated, then anesthetized with bicarbonate and preserved in 10% sugar-buffered formaldehyde (Haney and Hall, 1973). In the laboratory, zooplankton were counted and identified (see Table 1 for taxonomic groups; note rotifers were neither identified nor counted) using a subsample (1/32–1/16 of sample) of each vertical tow. Samples were split in order to expedite sorting time while still accounting for an accurate representation of the sample wherein subsamples contained at least 30 individuals from each designated taxon. We photographed and measured up to 20 individuals from each taxonomic group present in samples collected from the 15 m depth contour. We measured copepods from the tip of the head to the base of the caudal rami, nauplii from the tip of the head to the caudal base, cladocerans from the tip of the head to the base of the tail spine, and dreissenid mussel veligers from the anterior to posterior edge. We estimated dry weights of each zooplankter measured using published length–weight regressions adjusted for shrinkage in preservative (Table 1). We calculated mean daily biomass estimates for each zooplankton group by multiplying daily mean dry weights by densities.

To collect larval fish, we towed a bongo sampler (two 0.6 m diameter, 1.0 m long ichthyoplankton nets mounted on a single frame, 335 μm and 500 μm mesh, respectively) parallel to shore along three discrete depth contours (7 m, 15 m, and 18 m). Each tow lasted 10 min at 2–2.5 knots and ranged no further than 1500 m on either side of a pre-defined center point (Fig. 1). We performed replicate tows at each depth contour, targeting depths just below the surface of the water and every 5 m down in the water column (i.e., two tows at the 7 m depth, three tows at the 15 and 18 m depths). We attached a Sonotronics DTL sensor to the bongo sampler that recorded depth and temperature of each tow

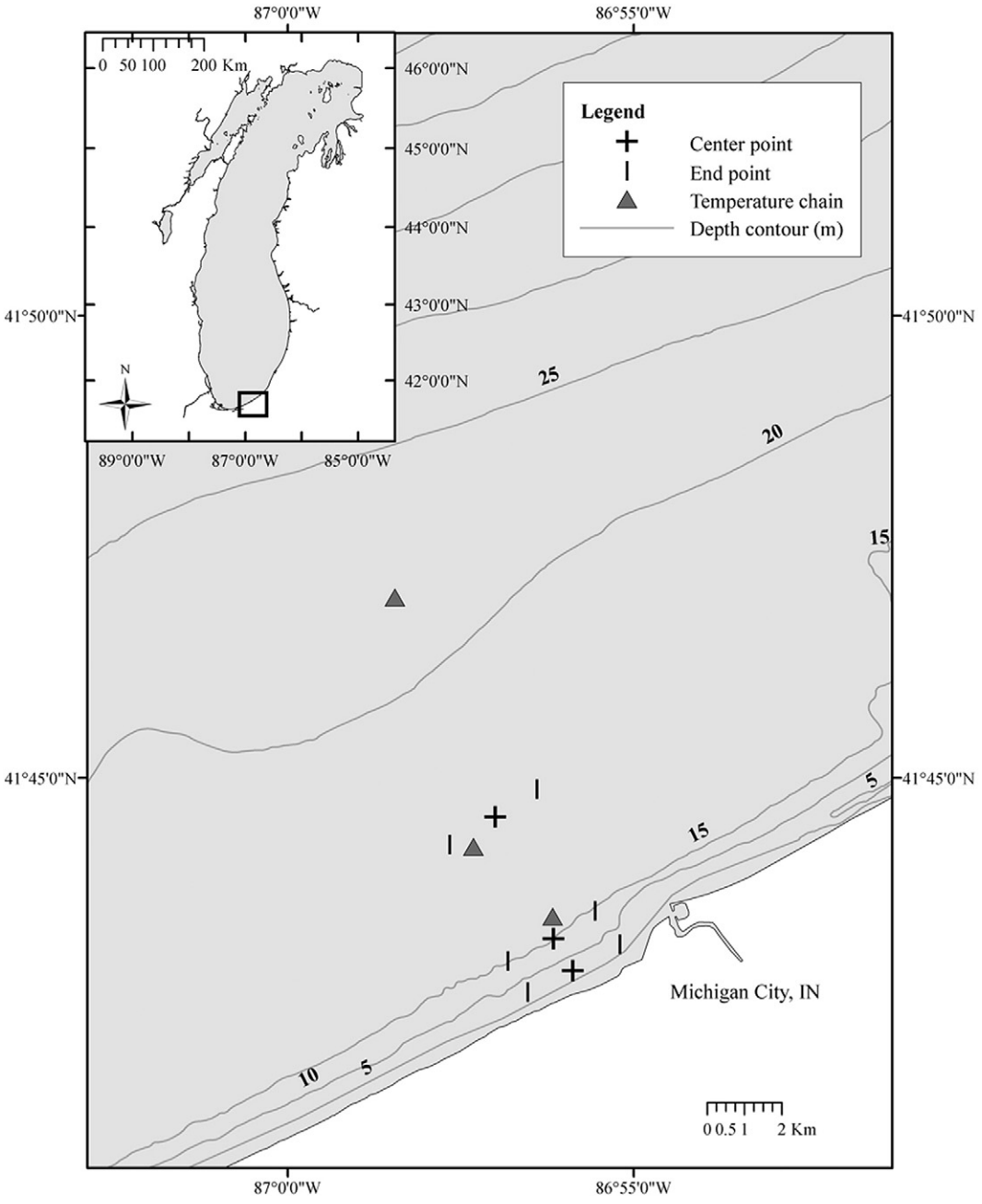

Fig. 1. Map of study location, including center and end points for field collections and location of moored temperature chains.

every 5 s in order to confirm we sampled desired depths. We also attached flow meters to the mouth of each net to estimate volume of water filtered during each tow. After each 10 min tow, we concentrated contents of each net and stored them separately in 95% ethanol. Though our nets did not have closing mechanisms and may have sampled the upper portion of the water column while setting and retrieving the nets, the relative volumes of water sampled while setting and retrieving the nets were roughly comparable among tows, and on average accounted

Table 1
Taxonomic groups identified, and parameters used to estimate dry mass from measured lengths, corrected for shrinkage using a correction factor, using the equation $M = aL^b$, where M = mass and L = length, in vertical zooplankton tows and larval yellow perch and larval alewife diet samples. Note that different groups were identified to different taxonomic resolution.

Taxa	a	b	Units	Source of L–W equation	Correction factor	Source of correction factor
Bosmina spp. (without eggs)	26.6	3.13	mm, μg	Dumont et al., 1975	33.1%	Pakhomov, 2003
Bosmina spp. (with 4+ eggs)	108.00	4.27	mm, μg	Dumont et al., 1975	33.1%	Pakhomov, 2003
Calanoida	0.00077	2.33	mm, μg	Dumont et al., 1975	37%	Giguère et al., 1989
Copepod nauplii	0.000011	1.89	μm, mg	Dumont et al., 1975	43%	Giguère et al., 1989
Cyclopoida	5.6713	1.9347	μm, μg	Dumont et al., 1975	37%	Giguère et al., 1989
Daphnia spp.	0.000000095	2.56	μm, μg	Dumont et al., 1975	28.2%	Pakhomov, 2003
Dreissena veliger	0.000000627	2.60	μm, μg	Sprung, 1984	0%	Pichlová-Ptáčníková and Vanderploeg, 2009

for 10% of total sample volume (J. Withers, Purdue University, West Lafayette, unpublished data).

We sorted larval fish samples under a dissecting microscope and identified individuals to lowest taxonomic level, usually species, using keys in Auer (1982). We photographed and measured total lengths (±0.01 mm) of up to 30 larval yellow perch and 30 larval alewives per tow. Measured total lengths were corrected for shrinkage in ethanol (Foley et al., 2010). We quantified diets of larval yellow perch and alewife for a subset of dates sampled. In order to capture temporal variation, we selected dates which spanned the time of larval emergence and when we collected relatively high numbers of larval yellow perch and alewife (yellow perch: DOY 152, 155, 161, 169 in 2010 and 158, 164, 171, 199 in 2011; alewife: DOY 155, 173, 195 in 2010 and 171, 186, 199 in 2011). To ensure adequate sample size (n > 30), we pooled individual larvae collected at all three depth contours (7 m, 15 m and 18 m) on some dates. We identified, enumerated, and measured lengths (±0.01 mm) of items found within the digestive tract of up to 30 yellow perch and 30 alewives per day to major taxonomic groups (Table 1) using the same techniques described above.

To estimate ages of larval fish, we extracted sagittal otoliths of any larva that no longer had a yolk sac and/or had identifiable items in their dietary tract. We mounted otoliths on a slide with Crystalbond™ epoxy, then counted daily growth increments using transmitted light under a compound microscope at a magnification of 40× or 60×. Daily growth increments were assessed by two independent readers with interpretation beginning at the center of the nucleus and progressing outward toward the distal edge of the otolith. If there was a discrepancy between readers, a third reader was used to assign the fish's estimated age. We estimated age (in days) of each larva by adding 2 days to the total number of increments (Höök et al., 2007; Roswell, 2012).

Data analysis

Field and laboratory sampling was intended to describe environmental conditions and densities, sizes, and diets of larval fish in the nearshore zone, as well as to provide input for habitat quality modeling (see below). To facilitate appreciation of environmental patterns, we conducted a series of analyses to explore spatial variation of ambient environmental conditions (i.e., water clarity and temperature) within the nearshore region. Similarly, we compared the mean densities of larval yellow perch and alewife a) between the 2 years and b) among bathymetric depths within years. To relate prey availability and prey consumed, we compared mean sizes among zooplankton taxa and contrasted the sizes of zooplankters consumed by larval fish versus sizes of zooplankters available in the environment. In addition, we quantified selection by larval yellow perch and alewife of various potential prey.

We used a repeated measures analysis of variance (ANOVA) to evaluate differences across bathymetric depths, and used Tukey's Honestly Significant Difference (HSD) test for post-hoc comparisons. Using Mauchly's test of sphericity (Mauchly, 1940), we found that the assumption of sphericity was not met for many analyses, so we performed a Greenhouse and Geisser correction (Greenhouse and Geisser, 1959). We compared mean Secchi depths, larval fish densities, and larval fish total lengths among bathymetric depths (7 m, 15 m, and 18 m) and compared mean daily temperatures among bathymetric depths (15 m, 18 m, and 21 m) during 2010 and 2011. Note that only temperatures between the surface and 15 m below the surface were used in order to make direct comparisons among bathymetric depths. Similarly, we used repeated measures ANOVAs, with Greenhouse and Geisser corrections when needed and Tukey's HSD tests to compare zooplankton mean daily densities and lengths across taxa.

We used Bonferroni corrected paired *t*-tests for inter-annual comparisons using 10 day means to pair data across years (e.g., mean daily larval yellow perch densities collected on DOY 140, 144, and 147 were averaged and classified as period 145). Specifically, we compared mean temperatures, Secchi depths, zooplankton densities and total lengths, and larval fish densities and total lengths between years.

To evaluate prey size selection for different prey we used a paired *t*-test to compare differences in the daily mean size of the dominant prey item found within larval fish digestive tracts and the size of major prey items within the environment (i.e., measured in zooplankton tows). Finally, to quantify feeding selectivity of available prey (Table 1) by larval yellow perch and alewife we calculated Chesson's alpha (α)

$$\alpha_i = \frac{r_i}{n_i}\left[\sum_{j=1}^{m}\frac{r_j}{n_j}\right]^{-1}$$

where r_i = proportion of prey taxon i in the ingested food; n = proportion of prey taxon i available in the habitat; and m = number of prey taxa considered (Chesson, 1978) for the subsets of dates selected for diet analyses during 2010 and 2011.

Growth rate potential modeling

The lack of older larval yellow perch and alewife confounded our ability to estimate growth rates for exogenously feeding fish subjected to varying conditions in the nearshore zone. That is, as the majority of the fish collected were quite young (mean 4 days old), growth was still likely influenced by maternal or embryonic effects rather than environmental variability. In order to examine the potential effects of environmental conditions (temperature, light, and prey densities) on larval fish growth potential we employed a bioenergetics approach. Specifically, we used bioenergetics modeling (Hanson et al., 1997; Kitchell et al., 1977) to assess the value of copepod nauplii (a preferred prey item found in low abundance in the surrounding environment) and dreissenid veligers (the most abundant prey item found in yellow perch guts) as suitable prey for larval yellow perch and alewife. We calculated spatially- and temporally-explicit bioenergetics growth rate potential (GRP) by subtracting energy losses due to respiration, egestion, excretion, and specific dynamic action (i.e., digestion) from energy intake from consumption of different types of prey, taking into account effects of temperature and organism mass. GRP is a proxy for habitat quality, where higher values qualitatively indicate better habitat (Brandt et al., 1992).

We used GRP modeling to assess habitat quality during 2010 and 2011 for 7 mm, larval yellow perch and alewife (see Electronic Supplemental Material (ESM) Figure S1). We focus this analysis on yellow perch because we had more information regarding their prey consumption and prey availability. Larval alewife on the other hand often had empty digestive tracts or consumed diatom prey; we did not quantify diatom densities in the environment and energy density and digestibility of diatom prey are uncertain. We considered four scenarios and allowed model larvae to forage on either copepod nauplii or dreissenid veligers, with 1) a temperature- and body mass-specific consumption rate (p-value, the proportion of maximum daily consumption) which was modified by water clarity or 2) consumption modeled as a function of body mass, temperature, water clarity and prey densities (described below). Both laboratory (Graeb et al., 2004) and field data (Bremigan et al., 2003) indicate that small copepods (0–0.5 mm) are preferred prey for first-feeding by small (<10 mm) yellow perch larvae and in this study most non-veliger prey items consumed were copepods (see Results), so we used copepod prey to represent a typical larval fish diet. Dreissenid veligers were abundant in the diets of young yellow perch (see Results). Past studies suggest that larval alewives also consume nauplii and veligers (Heinrich, 1981; Mills et al., 1995), and thus we present similar modeling analyses for alewife (ESM Fig. S1).

To model GRP of larval yellow perch, we applied existing bioenergetics parameters (Post, 1990), and assumed a constant mass of 0.6 mg (~7 mm

length) and energy density of 2512 J g^{-1} wet mass. Prey energy densities were 2000 J g^{-1} wet mass for nauplii and 1900 J g^{-1} wet mass for veligers (Höök et al., 2008). We restricted modeling to the 15 m depth contour because we sampled both light and temperature throughout the water column continuously throughout each season at this depth and we judged that this depth contour provided an adequate representation of temporal and spatial variability in temperature and water clarity of the nearshore zone. We estimated GRP daily for fish from day 146 to 210 in a vertical column of water 15 m deep divided into 30 half-meter layers. In all modeled scenarios, we used temperature and water clarity data collected from the field. Temperatures were daily, depth-specific averages calculated from the thermistor string, with daily values between vertical data points interpolated linearly within a day.

Water clarity was modeled in two ways: using calculations from Secchi depths in 2010 and light meter readings in 2011. We used light meter data in 2011 because data coverage was more complete, giving a better representation of day-to-day variability. Comparisons between 2010 and 2011 are valid because we found high agreement between light meter readings and values calculated for 14 m depths from observed Secchi data in 2011 ($n = 7$, $r = 0.98$). We calculated light levels at depth z (I_Z, lux) from Secchi values using the equation

$$I_Z = I_0 e^{-KZ}$$

where I_0 is the light level (irradiance) just below the surface and K is the light extinction coefficient, with K calculated as

$$K = 1.7 \cdot Z_{SD}^{-1}$$

where Z_{SD} is the observed Secchi depth, a relationship developed by Poole and Atkins (1929) and shown to be general over a wide range of turbidity by Idso and Gilbert (1974). We assumed I_0 to be 30,000 lx (Cole et al., 1995). Secchi depths were not available for each day, so values between data points were linearly interpolated.

The effect of light level on consumption and resulting GRP of both yellow perch and alewife was modeled using a relationship relating light levels to reactive distances of larval yellow perch (Richmond et al., 2004)

$$L_E = D_R x (0.1 + x)^{-1}$$

where $x = \log_{10}$ (irradiance), D_R is species- and size-specific maximum reactive distance, and L_E is the light effect. The first model scenario calculated GRP using a maximum p-value of 0.7 (Post, 1990) multiplied by L_E. That is, we assumed that $D_R = 1$ such that L_E took values from 0 to 1 and p-values ranged from 0 to 0.7. The second model scenario calculated daily consumption based on observed prey densities. Larval fish were assumed to forage during day light (15 h) and consumption was calculated by multiplying temperature-dependent larval yellow perch or alewife swimming speed (Houde, 1969; Klumb et al., 2003), reactive area (using species- and size-specific reactive distance adjusted by the light level; Miller et al., 1993; Richmond et al., 2004), prey density, and a capture success term (0.94 for both species; Richmond et al., 2004). If daily consumption exceeded bioenergetically-defined maximum potential consumption, it was set to this maximum potential value (Höök et al., 2008; Post, 1990).

Results

Thermal conditions near Michigan City displayed high temporal and spatial (horizontal and vertical) variation during both 2010 and 2011 and temperatures were on average warmer during 2010 as compared to 2011 (Fig. 2; $t_{169} = 14.67$, $p < 0.001$). Temperatures significantly differed across bathymetric depth contours in 2010 ($F_{1.05, 88.34} = 4.86$, $p = 0.028$) and in 2011 ($F_{1,84} = 18.64$, $p < 0.001$) with temperatures at the 18 m depth contour (mean temperature at 18 m = 15.9 °C) being significantly warmer than temperatures at the 15 m depth contour (15 m = 15.2 °C) in 2010 and temperatures at the 15 m depth contour (mean temperature = 13.6 °C) being significantly warmer than temperatures at the 18 m depth contour (18 m = 13.4 °C) in 2011. When considering temporal variation recorded by a single temperature logger at a static depth, the mean difference between maximum and minimum water temperatures recorded within 1 h was 0.2 °C in both 2010 and 2011, and the maximum hourly difference was 14.6 °C and 11.5 °C, respectively. Similarly, the average difference in mean daily temperature between consecutive days was 0.8 °C in 2010 and 2011 while maximum difference between consecutive days was 13.6 °C and 12.9 °C, respectively. These sharp changes in temperature at fixed locations reflect high-frequency thermocline oscillations and occasional influxes of cold/warm water from near-inertial waves and up/downwelling events, respectively (Troy et al., 2012). The aforementioned maximum hourly temperature change observed in 2010 (14.6 °C) was associated with the upwelling event at the 21 m depth contour on DOY 205 (10.4 °C to 24.9 °C). In total, thermal stratification was relatively inconsistent in the nearshore zone. However, stratification was most consistent and apparent farther offshore (21 m depth contour) and seemingly became established later in the year during 2011, as compared to 2010.

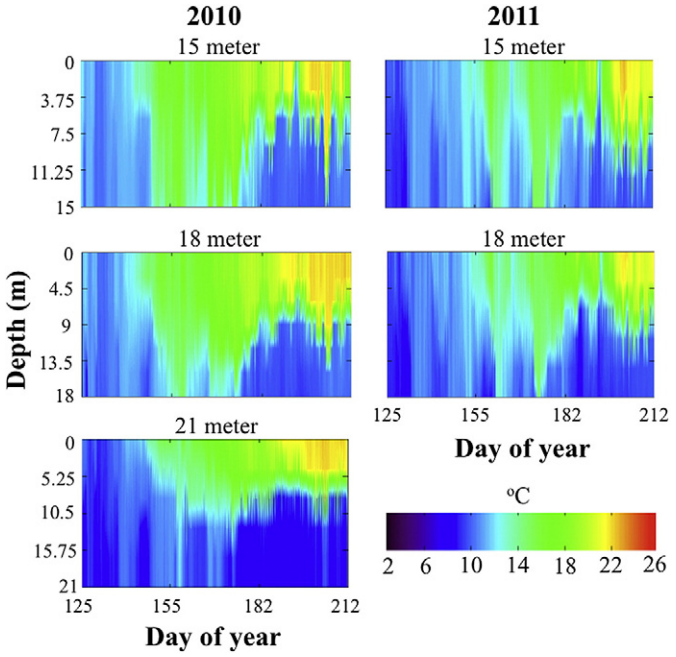

Fig. 2. Temperature profiles from nearshore Lake Michigan thermistor strings set at 15 (top row), 18 (middle row), and 21 m (bottom row) contour depths during 2010 (left column) and 2011 (right column). Cooler, darker tones represent colder temperatures and warmer, lighter tones represent warmer temperatures. Note the different depth scales across the three sampling depths.

Secchi depth did not significantly vary between 2010 and 2011 ($t_{16} = 1.16$, $p = 0.265$) but generally increased with bathymetric depth in both 2010 and 2011 (2010, $F_{2, 24} = 10.84$, $p < 0.001$; 2011, $F_{2, 12} = 4.27$, $p = 0.040$; Fig. 3). Moreover, during 2011, water clarity generally increased during the sampling period, while during 2010 this seasonal increase was less apparent. Light meter readings along the 15 m depth contour during 2011 corroborated Secchi disk measurements (Fig. 3) and also indicated that light penetration increased as the season progressed (Withers, 2013). The higher-resolution data from 2011 also highlights light level fluctuations on sub-weekly timescales.

Zooplankton densities and biomasses peaked in early July in 2010 and in mid-July in 2011 (Fig. 4). Peak total zooplankton densities were higher in 2010 than in 2011 (40,000 individuals m^{-3} in 2010 and

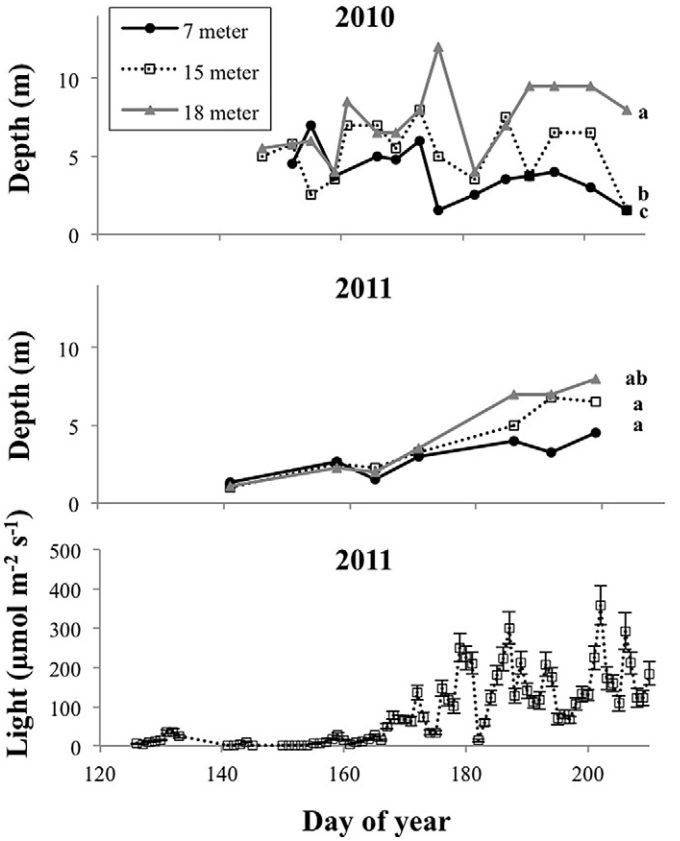

Fig. 3. Secchi depth (m) from 7, 15, and 18 m depth contours during 2010 (top graph) and 2011 (middle graph) and daily mean light meter readings at the 15 m depth from 2011 (bottom graph). Error bars represent one standard error.

around 25,000 individuals m^{-3} in 2011; Fig. 4). We observed greater mean densities of zooplankton in 2010 than 2011 ($t_{35} = 3.20$, $p = 0.003$) but found no differences in total lengths across years ($t_{29} = 1.52$, $p = 0.140$). There were significant differences in abundances of different zooplankton taxa in 2010 ($F_{1.63, 19.53} = 13.93$, $p < 0.001$) but not in 2011 ($F_{1.09, 6.55} = 3.04$, $p = 0.127$). Dreissenid mussel veligers had the greatest densities within the nearshore region on most sampling dates. Calanoids and copepod nauplii were the next most abundant taxa followed by bosminids and cyclopoids. *Daphnia* spp. densities were consistently low throughout 2010 and 2011 (Fig. 4). Mean size of zooplankters collected from the 15 m depth contour varied among taxa in 2010 ($F_{5, 15} = 32.92$, $p < 0.001$) and in 2011 ($F_{4, 24} = 64.79$, $p < 0.001$). With the exception of calanoids, mean size of each category of zooplankters in the environment generally remained relatively constant throughout 2010 and 2011 (Fig. 5). Copepod nauplii and dreissenid mussel veligers were consistently the smallest organisms and calanoids and *Daphnia* spp. were consistently the largest (Fig. 5).

We collected larval yellow perch and alewife between day 125 and 201 in 2010, and 158 and 199 in 2011 (Figs. 6, 7, and 8). Earlier emergence of fish can likely be attributed to warmer temperatures during 2010 (Fig. 2). We also observed higher densities of both larval yellow perch and alewife in 2010 than in 2011; though, only larval alewife densities were significantly greater in 2010 than 2011 (larval yellow perch; $t_{20} = 1.58$, $p = 0.131$; larval alewife; $t_{20} = 3.67$, $p = 0.002$). Peak densities occurred earlier and at a greater mean density in 2010 (Figs. 6, 7, and 8). Larval alewife densities did not vary with bathymetric depth in 2010 or 2011 (2010: $F_{1.31, 7.88} = 2.16$, $p = 0.149$; 2011: $F_{1.06, 6.36} = 2.54$, $p = 0.159$), while larval yellow perch densities increased with bathymetric depth in 2010 ($F_{1.11, 21.02} = 4.22$, $p = 0.049$), but not in 2011 ($F_{2, 12} = 0.76$, $p = 0.490$).

Larval yellow perch sampled during 2010 and 2011 were small (3.6–11.5 mm; mean 6.3 mm) and young (age of feeding larvae ranged between 0 and 6 days old; mean 4 days old). While larval alewife had a broader size (3.0–26.1 mm) and age (age of feeding larvae ranged between 0 and 19 days old) distribution during both years, the mean size (7.0 mm) and age (6 days old) of alewife were also low (Table 2). Total lengths of larval yellow perch and alewife did not significantly differ across bathymetries in 2010 and 2011 (larval yellow perch 2010; $F_{2, 10} = 2.03$, $p = 0.183$; larval yellow perch 2011; $F_{1.00, 3.00} = 3.46$, $p = 0.160$; larval alewife 2010; $F_{1.15, 13.76} = 3.66$, $p = 0.072$; larval

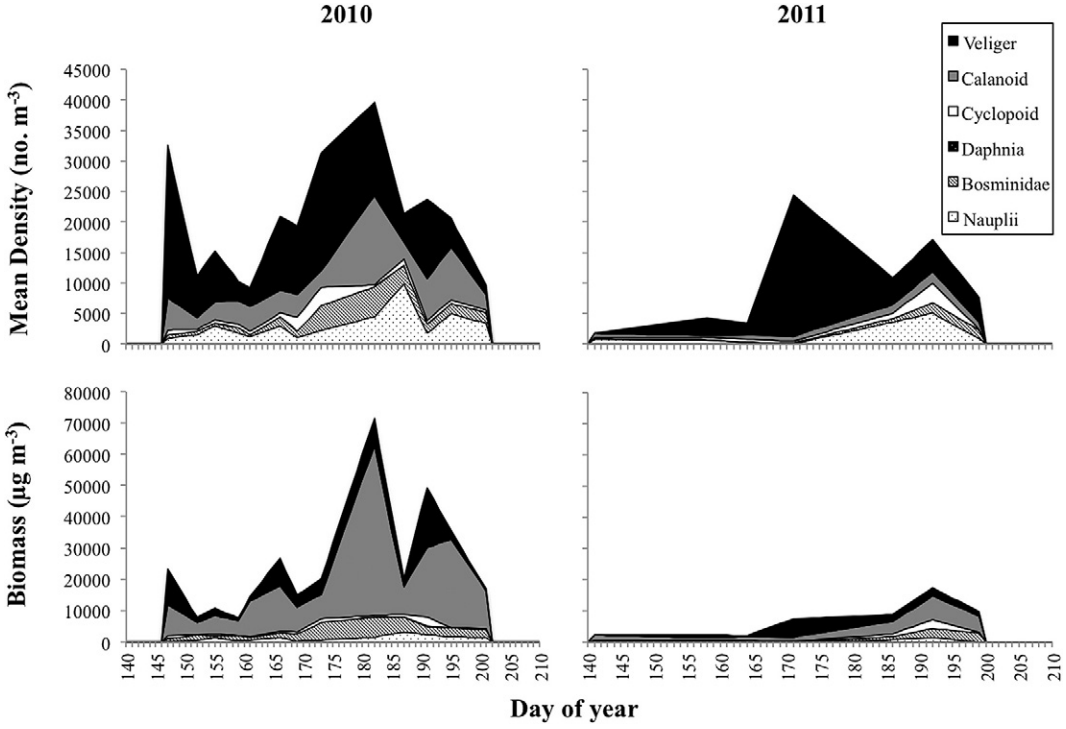

Fig. 4. Mean zooplankton density (top row) and biomass (bottom row) for 2010 (left column) and 2011 (right column).

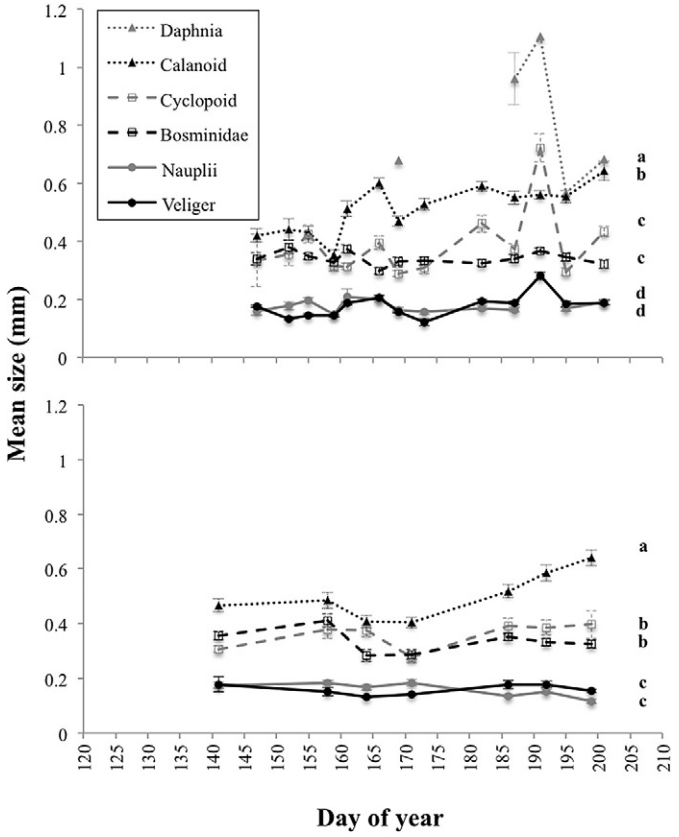

Fig. 5. Daily mean size (mm; ±SE) of zooplankters collected in vertical zooplankton tows (64 μm) from the 15 m bathymetric depth contour during 2010 (upper panel) and 2011 (lower panel). Letters denote significantly different sizes based on post-hoc analyses.

alewife 2011; $F_{2,6} = 1.16$, $p = 0.375$) and did not vary inter-annually (larval yellow perch: $t_{11} = 0.36$, $p = 0.724$; larval alewife: $F_{10} = 0.80$, $p = 0.445$). We collected many small, young larval yellow perch and alewife transitioning from endogenous to exogenous feeding. The majority of larval yellow perch and alewife examined were either yolk sac larvae or contained no prey in their digestive tracts (yellow perch 2010: 353 out of 500; 2011: 138 out of 172; alewife 2010: 532 out of 647; 2011: 108 out of 119). In particular, many alewife larvae had no prey in their gut: 422 of 537 (79%) post yolk sac alewife larvae were empty during 2010 and 72 of 83 (87%) during 2011, as compared to 168 of 313 (54%) post yolk sac yellow perch larvae during 2010 and 40 of 74 during (54%) 2011. As the season progressed in both 2010 and 2011, the proportion of larval yellow perch and alewife with prey in their digestive tracts increased. Nonetheless, on each sampling date examined in 2010 and 2011, only 18–58% and 15–29% of post yolk sac larval yellow perch and alewife, respectively, contained prey in their digestive tracts.

For larval yellow perch that did have material in their digestive tracts, dreissenid mussel veligers constituted >98% and >97% of diet items in 2010 and 2011, respectively. Yellow perch also ingested diatoms (mainly *Fragilaria* spp.), dreissenid mussel trochophores, copepod nauplii, cyclopoids, and calanoids. The relatively high prevalence of veligers in diets was not simply a reflection of their densities in the environment, as yellow perch displayed consistent positive selection for veligers (Table 3). However, there was no evidence of size-selective consumption of veligers, as mean total lengths of dreissenid mussel veligers ingested by larval yellow perch were not significantly different from lengths of dreissenid mussel veligers caught within vertical zooplankton tows in either year (2010, $t_4 = 2.84$, $p = 0.167$; 2011, $t_3 = 0.27$ $p = 0.639$). Larval alewife predominantly preyed upon diatoms (mainly *Fragilaria* spp.) though we also found dreissenid mussel veligers, copepod eggs, copepod nauplii, and calanoids in some digestive tracts (Table 2; Table 3).

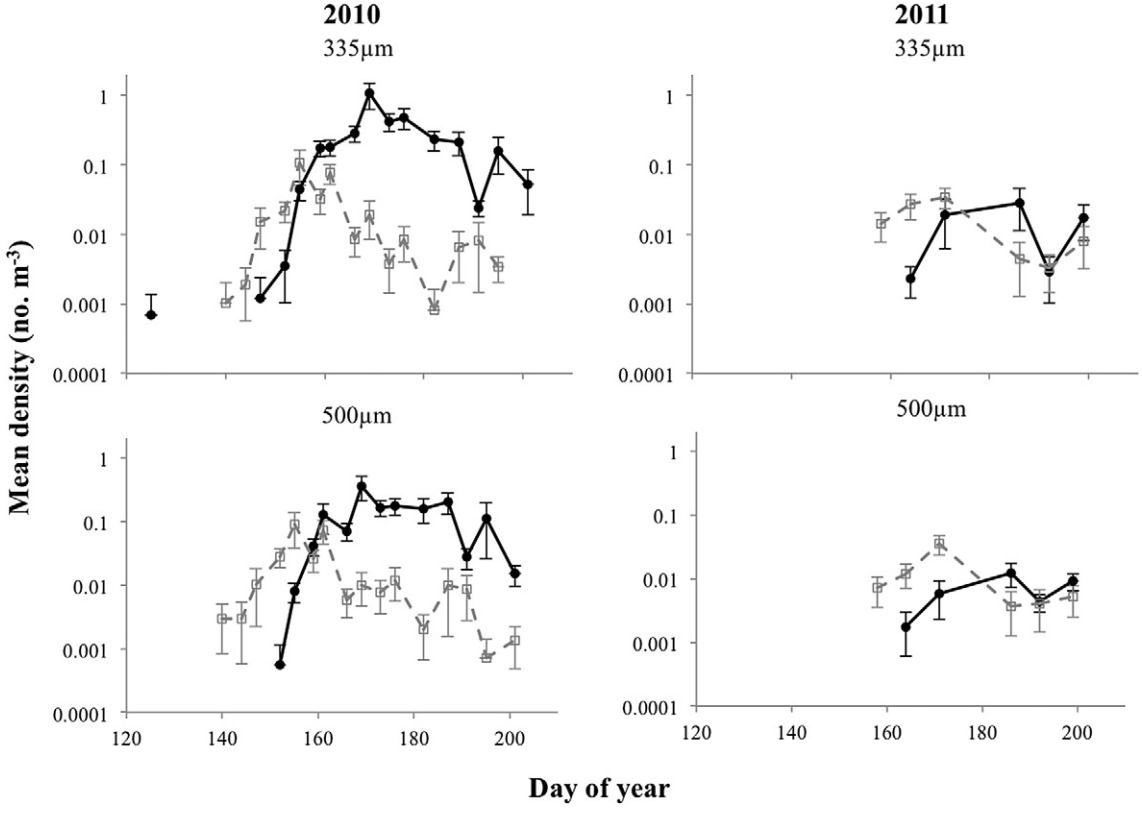

Fig. 6. Log mean density (no. m^{-3}; ±SE) of larval yellow perch (gray squares) and larval alewife (black circles) collected in the 335 (top row) and 500 μm (bottom row) bongo sampler during 2010 (left column) and 2011 (right column). Error bars denote one standard error. Note that densities are presented for dates when >0 larval fish were collected.

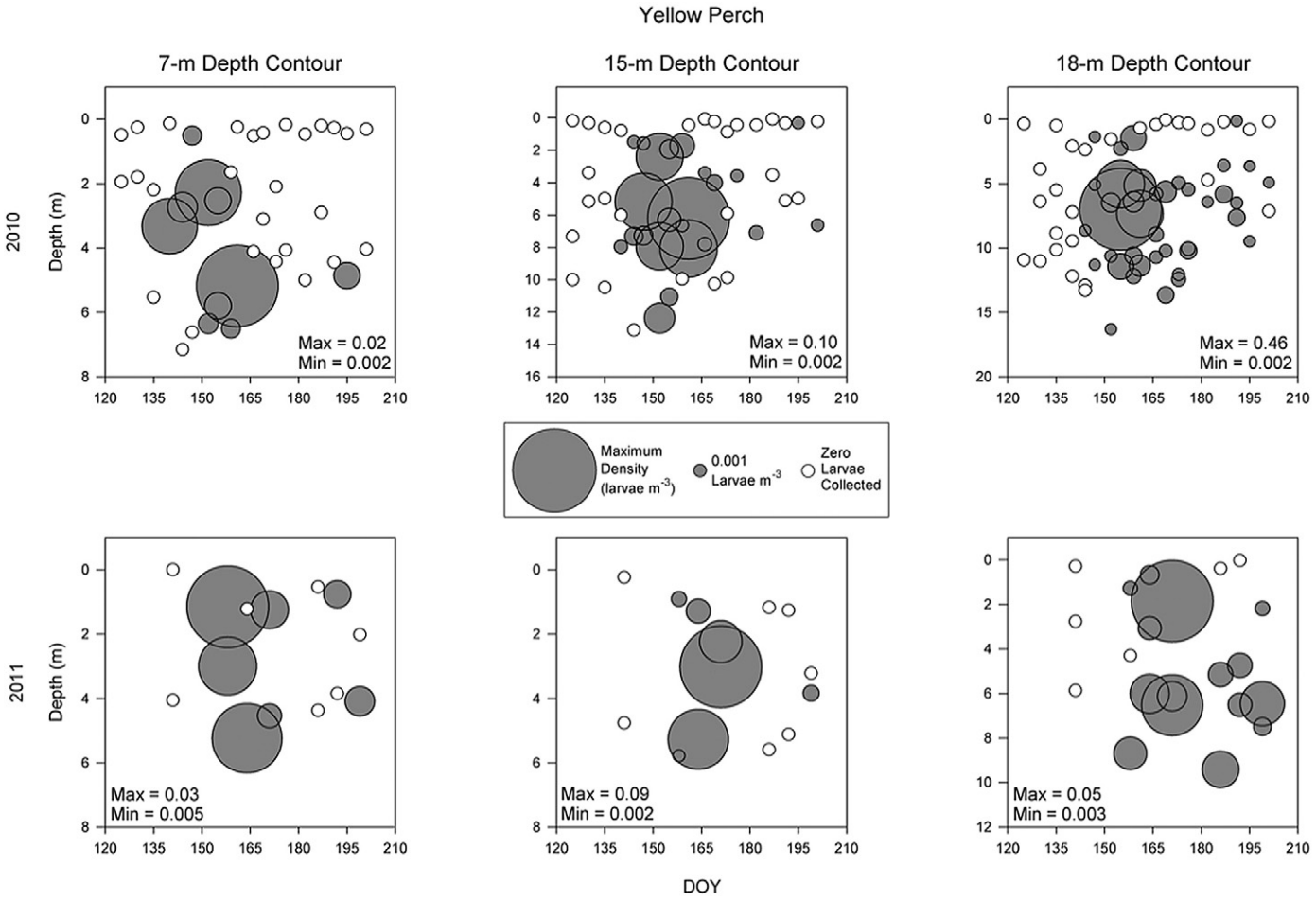

Fig. 7. Densities of yellow perch larvae collected in the bongo sampler during 2010 (upper row) and 2011 (lower row). The size of the bubbles indicates density, averaged between the 335 μm and 500 μm mesh sizes, and is scaled to the maximum density observed at that date-depth combination. Gray bubbles show when larvae were collected, and white bubbles mean that no larvae were collected in the bongo sampler for that date–depth combination.

For GRP model scenarios in which habitat quality was calculated as a function of temperature and light (i.e., assuming prey consumption was not related to ambient prey densities) habitat quality for both larval yellow perch and alewife was moderately high when either nauplii or veligers served as model prey. However, when consumption varied according to observed prey densities, the relatively high abundance of veligers relative to nauplii produced a clear increase in habitat quality during both 2010 and 2011 (Fig. 9 and ESM Fig. S1). The most striking effect of relatively high veliger densities in the model was to predict a positive growth environment for larval yellow perch in both years that would not have existed if nauplii were the only modeled prey source (Fig. 9). In addition to the influence of prey densities, abiotic conditions strongly affected habitat quality. Cool temperatures early in 2011 contributed to poor habitat quality, especially when combined with low water clarity early in the season (Fig. 9 and ESM Fig. S1). Habitat quality was highly variable from day to day, and responded to rapidly-changing temperatures, sometimes resulting in much or all of the water column shifting from favorable to unfavorable habitat conditions for several days.

Discussion

As described in previous studies (e.g., Ayers et al., 1958; Mortimer, 2004; Troy et al., 2012), we documented high variation of environmental conditions in a nearshore region of Lake Michigan. Thus, our results suggest that young yellow perch and alewife, which initiate exogenous feeding in this region, may be exposed to highly favorable or unfavorable conditions in terms of both biotic (i.e., availability of suitable prey) and abiotic (i.e., light and temperature) factors depending on the timing and location of their emergence. Over the past 20–30 years, reductions in nutrient loading and activities of invasive species, in particular dreissenid mussels, may have enhanced the relative importance of the nearshore zone to lake-wide production and biotic interactions in Lake Michigan (Hecky et al., 2004; Madenjian et al., 2002; Turschak et al., 2014) by modifying biotic and abiotic factors acting in both the nearshore and offshore zones of Lake Michigan (Dettmers et al., 2003; Hecky et al., 2004; Vanderploeg et al., 2002). While invasive species may have contributed to a decrease in densities of primary producers (Mida et al., 2010) and restructuring of the Lake Michigan zooplankton community (Vanderploeg et al., 2012), they also may provide an important prey source for early feeding larval yellow perch and alewife. Specifically, we found that both small larval yellow perch and alewife actively consumed dreissenid veligers, with veligers constituting the vast majority of prey items consumed by small larval yellow perch. Modeled growth rate potential supports the hypothesis that veligers could be a viable prey source due to their abundance. However, the digestibility and nutritional content of veligers for larval yellow are largely unknown. Further, prey resources may have been limiting (as evidenced by a high frequency of empty digestive tracts for both larval yellow perch and alewife). Thus, while it is clear that habitat conditions were highly variable for larval yellow perch and alewife in this nearshore zone of Lake Michigan, it is an open question how well larval fish perform in the nearshore zone and this may ultimately be dependent on their ability to effectively utilize these small prey.

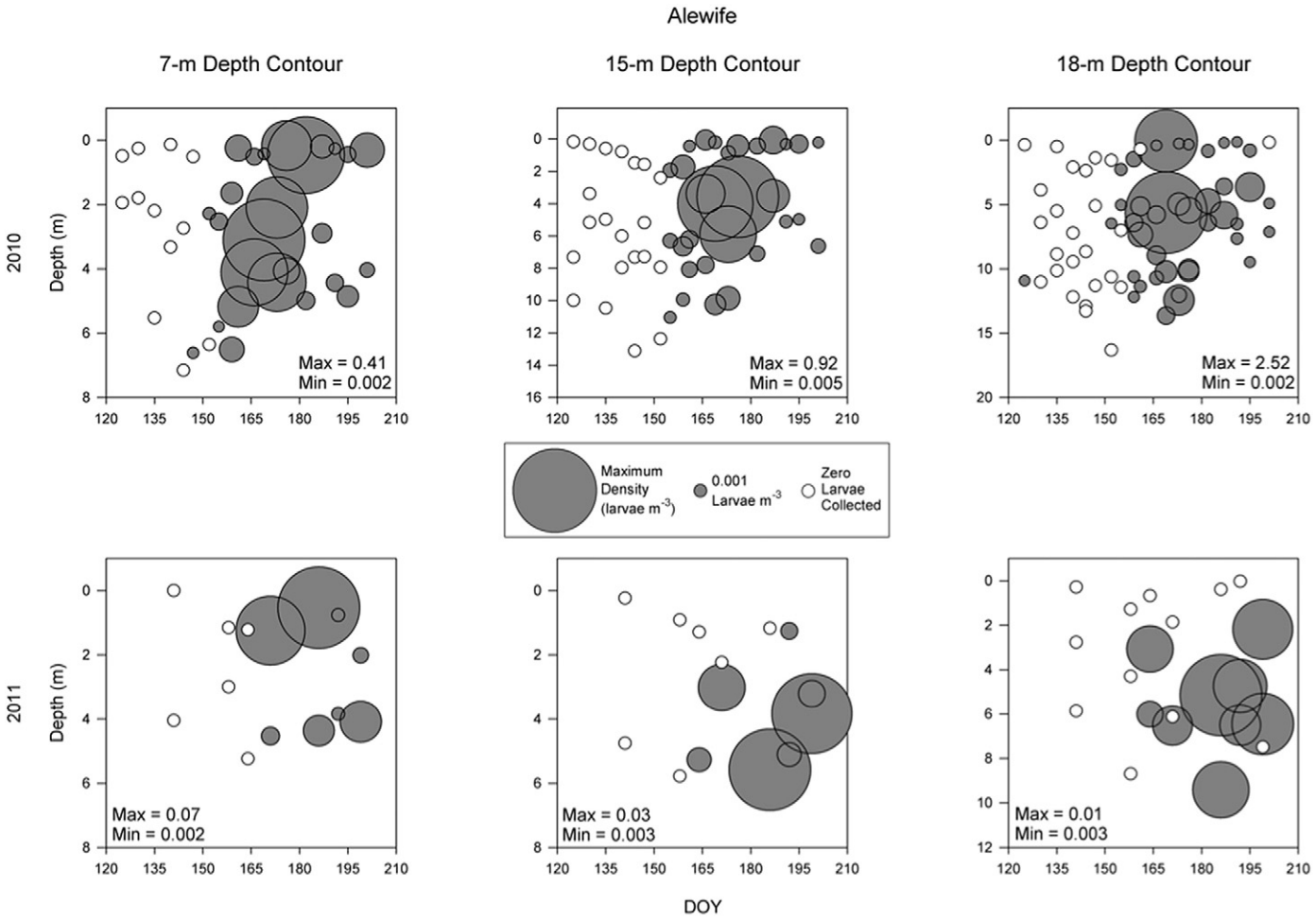

Fig. 8. Densities of alewife larvae collected in the bongo sampler during 2010 (upper row) and 2011 (lower row). The size of bubbles indicates density, averaged between 335 μm and 500 μm mesh sizes, and is scaled to the maximum density observed at that date–depth combination. Gray bubbles show when larvae were collected, and white bubbles mean that no larvae were collected in the bongo sampler for that date–depth combination.

Our examination of fish diets revealed high numbers of dreissenid mussel veligers in larval yellow perch and diatoms and veligers in larval alewife. Contrary to these results, we expected larval yellow perch and alewife to prey primarily upon copepod nauplii, copepod adults, and rotifers during their first few days of feeding. Other studies have documented the presence of dreissenid veligers in Great Lakes larval fishes, however, in these studies, veligers only contributed a small percent of the total diets (Mills et al., 1995; Roswell, 2012). The implications for dreissenid mussel veliger ingestion are largely unexplored though the ingestion of adult dreissenid mussels by adult fish species has been attributed to decreased growth of some Great Lakes fishes (e.g., Pothoven and Madenjian, 2008, but see Madenjian et al., 2010). Larval yellow perch may be feeding on veligers because of their size or ease of capture, or simply because they are relatively abundant. Small larval yellow perch have been shown to be gape-limited (Bremigan et al., 2003; Schael et al., 1991). Veligers were the smallest prey items

Table 2
Contents of larval digestive tracts analyzed. "Other" category includes copepod eggs, cyclopoid copepods, calanoids copepods, and dreissenid mussel trochophores. Mean number of prey items per fish was 1.0.

Species	Year	Day of year	Total length (mm, range)	Mean age (days, range)	n Empty (Yolk sac)	n Empty (Post yolk sac)	n Feeding	% Veliger	% Nauplii	% Diatom	% Other
Yellow perch	2010	152	6.1 (4.2–7.4)	1.7 (0–4)	19	26	10	100%	0%	0%	0%
		155	6.3 (3.8–7.7)		78	64	36	69%	0%	11%	25%
		161	6.3 (3.6–8.5)	1.4 (0–4)	76	67	61	82%	0%	16%	7%
		169	6.6 (4.9–10.2)	1.7 (0–3)	12	11	40	98%	0%	0%	5%
	2011	158	6.2 (5.1–7.6)	1.7 (0–3)	15	9	2	100%	0%	0%	0%
		164	6.4 (5.4–7.4)	1.1 (0–2)	36	9	3	100%	0%	0%	0%
		171	6.2 (4.8–7.9)	1.6 (0–3)	45	16	22	95%	5%	0%	9%
		199	6.7 (5.4–11.5)		2	6	7	86%	0%	0%	14%
Alewife	2010	155	5.1 (3.0–9.4)	1.8 (0–4)	51	34	6	17%	0%	50%	33%
		173	7.0 (3.5–17.7)	0.3 (0–1)	19	304	75	21%	1%	57%	31%
		195	6.7 (3.4–15.1)	3.3 (0–11)	40	84	34	12%	0%	79%	9%
	2011	171	5.1 (3.8–8.4)	0.4 (0–2)	12	20	1	0%	0%	100%	0%
		186	5.7 (3.7–11.8)	3.4 (0–10)	23	25	2	0%	0%	50%	50%
		199	9.0 (4.0–25.3)	5.4 (0–17)	1	27	8	38%	0%	38%	50%

Table 3
Chesson's alpha selectivity index for larval yellow perch and larval alewife sampled in nearshore Lake Michigan in 2010 and 2011. Copepod eggs and unidentifiable items were not incorporated in these analyses since their densities were not quantified within the environment. Note that although diatoms were frequently found within larval alewife gut contents, they were not quantified and were therefore not included in these indices.

Mean prey-specific α selectivity values								
Species	Year	Day of year	Nauplii	Bosminidae	Daphnia	Cyclopoid	Calanoid	Veliger
Yellow perch	2010	152	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
		155	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
		161	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.009 ± 0.01	0.99 ± 0.01
		169	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
	2011	158	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
		164	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
		171	0.026 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.018 ± 0.02	0.003 ± 0.00	0.95 ± 0.05
		199	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
Alewife	2010	155	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
		173	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.11 ± 0.08	0.89 ± 0.08
		195	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
	2011	199	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00

found within our zooplankton samples and were comparable in size to copepod nauplii, previously shown to be preferred prey for first-feeding yellow perch (Bremigan et al., 2003; Graeb et al., 2004). Furthermore, encounter and capture rates of veligers by larval fish would presumably be relatively high due to veligers' slow mobility, relatively prominent visibility, and high densities within the nearshore region (Fig. 4). Assuming that veligers are digestible by larval fish, our model results indicate that they could be a valuable alternative prey during the critical early period of life.

An important unanswered question regarding the ingestion of veligers by larval fish relates to veliger digestibility and overall energetic value. The majority of veligers' shells found within digestive tracts of larval fishes examined in the present study were intact and in good to excellent condition, but we did not assess presence or condition of veliger soft tissue. Presumably veliger soft tissue could be digested and the shell would be excreted. However, since the shells were usually found in excellent condition it is possible that shells prevent digestion of even soft tissues by larval yellow perch. If digestibility of veliger shells is low, gut fullness and excretion of shells may prove to be energetically demanding and could damage the fish's digestive tract. Conversely, dreissenid mussel veligers may be providing a substantial substitute prey base for first-feeding larvae, filling a void since the decline of many zooplankters beginning as early as the late 1980s (Dettmers et al., 2003). Feeding on veligers was shown to significantly enhance growth rates of larval *Prochilodus lineatus* (Paolucci et al., 2010), thus it is plausible that larval yellow perch are able to extract energy from this abundant food source. The lack of other diet items in the majority of yellow perch digestive tracts provides considerable evidence that larval yellow perch performance (growth and survival) is dependent upon their ability to utilize energy from dreissenid mussel veligers.

Early feeding alewife similarly demonstrated reliance on one major food source; however, it was not dreissenid mussel veligers, but rather diatoms. We believe alewife predation on diatoms was not accidental since most stomachs only contained diatoms and we found the same taxonomic group of diatoms, *Fragilaria*, in numerous alewife digestive tracts in both 2010 and 2011. Though others have found small alewife

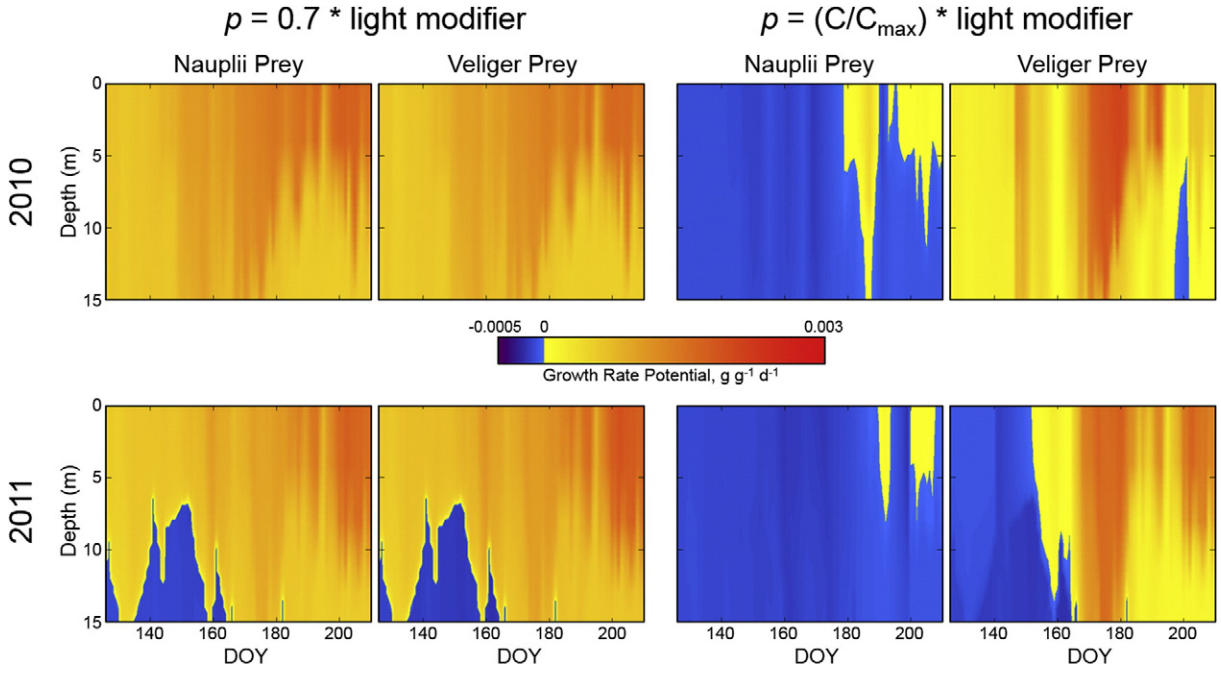

Fig. 9. Modeled growth rate potential (GRP) of larval yellow perch at the 15-m depth, offshore of Michigan City, IN. Panels show GRP calculated for 2010 and 2011 with either copepod nauplii or dreissenid veligers as prey. The four left panels use a base *p*-value (proportion of maximum daily consumption) of 0.7 multiplied by a light factor, and the four right panels use a variable *p*-value based on daily calculations of consumption driven by observed prey densities, also multiplied by the light factor. Warm, lighter tones represent positive GRP (good habitat) and cool, darker tones represent negative GRP (poor habitat).

preying upon rotifers and algae, which are similar in size to diatoms (Heinrich, 1981), and a recent study has shown that offshore *Mysis* spp. appear to feed on *Fragilaria* (O'Malley and Bunnell, 2014), to our knowledge, no studies have documented this level of consumption of diatoms by alewife. Larval Pacific herring (*Clupea pallasi*), which are con-familial with alewife, have been documented to prey upon diatoms, which, along with aloricate ciliates, may constitute the majority of their carbon intake (Friedenberg et al., 2012). Diatoms and other protists have been suggested to alleviate starvation when larger, preferred prey items are limited (Hunt von Herbing and Gallagner, 2000), as is possible in nearshore Lake Michigan.

Temperature undoubtedly also influences larval fish growth and survival. On average, southeastern Lake Michigan is the warmest region in the main basin of the lake due to its relative shallowness, southern location, and prevalence of cold upwelling events on the opposite, western side of the lake (Mortimer, 2004). These warm temperatures should facilitate relatively early spawning and hatching in this region, and indeed our findings suggest that near optimal temperatures for growth of both larval yellow perch and larval alewife are present in the nearshore zone. This can provide a recruitment advantage, as early hatchers may take advantage of early emerging zooplankton, reach a greater size by the end of the growing season, and reduce their potential for later size-dependent mortality (e.g., overwinter mortality; Höök et al., 2007; Höök and Pothoven, 2009). It is plausible that our study region constitutes a relatively important nursery region for young yellow perch and alewife. For example, yellow perch spawned in Illinois waters of Lake Michigan (Glover et al., 2008) could be rapidly carried by waters currents into our study area.

While this region of Lake Michigan is warm relative to the rest of the main basin, it is nonetheless highly variable. Cool nearshore temperatures contributed strongly to areas of modeled poor habitat quality, especially when combined with low water clarity and prey densities. In particular, during late spring variable temperatures contributed to highly variable habitat quality from day to day. This analysis demonstrates how small temporal shifts in the hatching of larval fish in the nearshore zone can strongly influence early life survival and ultimately, recruitment. While this variability is dampened when assuming constant prey availability, incorporating realistic prey densities into GRP calculations enhances the abiotic variability associated with the nearshore environment.

Growth rate potential was on average greater during 2010, than 2011. This is consistent with higher average temperatures and zooplankton densities during 2010. In addition, an earlier peak in zooplankton densities and earlier stratification at the offshore (21-m) site may have provided favorable conditions for early-stage larval yellow perch and alewife. Interestingly, larval alewife densities were also significantly greater in 2010 than in 2011 which is consistent with Warner et al. (2012), who documented that the 2010 alewife year-class in Lake Michigan was particularly strong. Thus, it is attractive to speculate that favorable conditions in nearshore, southeastern Lake Michigan, and perhaps other regions of the lake, contributed to high densities of early-stage larval alewife and ultimately led to a strong year-class. If so, annual alewife recruitment success in Lake Michigan could be determined during very early life. We believe that this possibility could be evaluated through future studies.

Though we suggest that dreissenid veligers and/or diatoms may provide the majority of energy to young larval fish caught in nearshore southern Lake Michigan, we found a high proportion of empty stomachs of larval yellow perch and alewife despite relatively early emergence, favorable temperatures, and prey densities similar to observations in previous studies (Dettmers et al., 2005; Pothoven and Fahnenstiel, 2015). The prevalence of empty stomachs of larval yellow perch and larval alewife in both 2010 and 2011 suggests starvation may be an important source of mortality in this region. We do not believe that the limited number of prey in larval digestive tracts simply reflects a methodological bias, as a recent study of larval yellow perch in Saginaw Bay, Lake Huron using near identical capture methods and identical laboratory methods yielded consistently high numbers of prey in larval yellow perch digestive tracts (Roswell et al., 2014). Moreover, others have documented similar results with a high frequency of empty digestive tracts of larval alewife in nearshore Lake Michigan (Höök, 2005) and larval yellow perch in Green Bay, Lake Michigan (Bremigan et al., 2003). Among feeding larvae that did have items within their stomachs, the most abundant prey items were among the smallest available in the environment, suggesting that gape size limitations influenced larval feeding behavior.

The preponderance of small, young larval fish likely reflects both a high abundance of small, young individuals in the nearshore zone and a response to sampling design. That is, we sampled during daytime, when larger larvae may be able to more effectively avoid sampling gear (e.g. Höök, 2005). Sampling during nighttime, using larger mesh nets and gear with larger capture surface areas may have led to capture of more larger, older larval fish (e.g., Höök, 2005; McGurk, 1992). Alternatively, larger and older larvae may have been advected offshore or along shore by mass water movement events within the first 1 to 3 weeks following hatching (Dettmers et al., 2005; Weber et al., 2011). If larval fish are quickly advected offshore, then the availability of suitable prey items in the volatile nearshore region may have less influence on growth and ultimate recruitment. However, if offshore advection is delayed, the conditions in the nearshore region may be extremely important to these fishes' growth and subsequent recruitment.

Fish collected during our study were also not uniformly distributed throughout the water column. There were no consistent trends in vertical distributions or distributions across depth contours during 2010 and 2011 (Figs. 7 and 8; Withers, 2013). Larval yellow perch and alewife collected from offshore waters are similarly not uniformly distributed throughout the water column, but instead concentrate in the epilimnion and near the surface (Martin et al., 2011; Nash and Geffen, 1991). Though our study suggests slight differences in temperature from top to bottom, particularly in the later months of sampling (Fig. 2), these nearshore, shallow sites are weakly stratified, with a diffuse thermocline, relative to the much stronger offshore stratification (Troy et al., 2012). Farther offshore, bottom waters are truly hypolimnetic, with temperatures near 4 °C, whereas the bottom waters at our sites were closer to 10 °C. We suggest that the lack of consistent thermal structure may have contributed to the less consistent vertical distributions of larval fish in the nearshore zone.

In conclusion, the southeastern nearshore (<20 m depth) region of Lake Michigan exhibits highly variable biotic (i.e. prey availability) and abiotic (i.e. temperature, light) conditions. Habitat quality of first-feeding larval yellow perch and larval alewife appear to be affected by these conditions, as lack of historically preferred prey and fluctuations in temperature seem to affect feeding. We found a large number of empty stomachs among the exogenously feeding larvae collected. Interestingly, among exogenously feeding larvae, dreissenid mussel veligers and diatoms constituted the highest occurrences among larval yellow perch and alewife diets, respectively. Dreissenid mussels have heavily altered the type and distribution of prey available to young larval fishes in the nearshore zone by altering prey communities and water clarity; however, the abundance of veligers and the potential for these to be important food sources for young fishes may buffer negative impacts of dreissenids on native zooplankton and bridge larval fish through a potential critical period (including perhaps the time between hatch and advection toward more favorable habitats). We suggest that future studies should examine the implications (i.e., energetic value and digestibility) of larval fish consumption of dreissenid mussel veligers, particularly for yellow perch. Moreover, because small larval alewife seemed to target diatom prey, the consequences of this foraging strategy should be considered. Our results may further suggest that dreissenids are “not a dead end in Great Lakes food webs” (Madenjian et al., 2010).

Acknowledgements

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Appendix A. Alewife growth rate potential modeling

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2015.08.003.

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